
PREVAILING SCENARIOS OF FUNCTIONAL CHANGE IN ANTHROPOCENE BIRD AND MAMMAL COMMUNITIES

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Abstract

Aim: Despite unprecedented environmental change due to anthropogenic pressure, recent work has found increasing species turnover but no overall trend in species diversity through time at the local scale. Functional diversity provides a potentially powerful alternative approach for understanding community composition by linking shifts in species identity to mechanisms of ecosystem processes. Here we present the first multi-taxa, multi-system analysis of functional change through time.

Location: Global, with a North American focus

Time period: 1923-2014

Major taxa studied: Mammals, Birds

Methods: We paired thousands of bird and mammal assemblage time series from the BioTIME database with existing trait data representative of a species' functional role to reconstruct time series of functional diversity metrics. Using generalized linear mixed models we estimated general trends in those metrics and trends for individual studies.

Results: We found no overall trend in any functional diversity metric, despite data replicating species-based patterns of constant richness with increasing turnover. The lack of trend held even after correcting for changes in species richness. At the study-level, we identified four prevailing scenarios of species and functional change, which showed links to the duration of the observation window.

Main Conclusions: General trends indicate that on the aggregate one type of functional shift is not more prevalent than the other across many taxa, biomes, and realms. At the study-level, there were also a substantial number of time series exhibiting no species or functional change, however the majority of studies showed a shift in a species or functional metric. With no one prevailing scenario of change, it will be critical to link change scenarios to drivers of change, particularly to identify communities with capacity to resist drivers from those not experiencing substantial pressure from a driver.

Keywords biodiversity change · functional traits · global change · time series

1 Introduction

Ecological communities are experiencing unprecedented change as a result of anthropogenic pressures such as climate change, land use change, and invasive species. Impacts of these pressures are well documented at a global scale by an accelerating global extinction rate (1), and fundamental changes in some of the most well-studied systems (e.g. coral bleaching, 2). At the local scale however, species diversity tells a different story. Recent syntheses of local trends in biodiversity over time have found no net change in local species diversity despite ongoing turnover (3–6) and evidence of significant shifts in community composition underlying consistent species richness (7–9). While communities are clearly changing, our most common species-based approaches do not fully capture the nature of that change.

The meaning of general trends derived from limited data, and their relevance for conservation, is a topic of on going debate. Global analyses have been heavily criticized for geographic biases, lack of data in the most heavily impacted areas, and not taking into account the ecological context of individual studies (10–12). Many of these criticisms reflect limitations of ecological data on the whole, and proponents argue we must make the best of the imperfect data available (13). Still, there is general consensus on a few local-scale patterns that seem to be characteristic of the anthropocene, including the prevalence of species turnover across communities and patterns of both richness increase and decrease in different taxa and biomes (14). Understanding the implications of change in species assemblage for ecosystem stability and function is a critical next step in moving forward the biodiversity change conversation.

Functional diversity offers a potentially powerful alternative to species-based approaches for detecting and describing community change by providing a mechanistic link between species’ response to environmental change (*response traits*) and the processes they perform (*effect traits*) (15–17). By describing the functional trait space, functional diversity metrics capture the disproportionate impact of losses or gains of functionally unique species. Functional diversity metrics are therefore particularly well suited for assessing community shifts underlying even constant species richness trends.

Beyond simply characterizing changes in community structure, trends in functional composition also have important implications for ecosystem stability, function, and resilience. There is increasing evidence functional diversity is a better predictor of ecosystem function than species-based metrics (18, 19), and that different facets of functional diversity play essential roles in maintaining ecosystem stability (20, 21). Almost all hypothesized mechanisms underpinning the relationship between species diversity and ecosystem function are trait-dependent (22). Determining functional trends therefore gives a more direct picture of potential trends in critical ecosystem processes.

It is critical to establish whether or not functional loss is prevalent across communities. While functional loss is frequently cited as one of the most pressing concerns of the anthropocene (23–25), local-scale loss is not necessarily inevitable even in scenarios of species loss (26, 27). Forecasts of functional loss range from negligible (28) to dire (29, 30). And while some observed trends show significant functional loss (31) others document no loss even in some of the most heavily impacted communities (32–34). On paleoecological time scales functional composition shows mixed responses to environmental change and extinction events (35, 36), with significant impacts of species extinctions on functional diversity in some taxa and not others (37). For some time periods, functional structure appears to be maintained for substantial portions of geological time (38). Still, some losses of functional diversity are indisputable on both paleoecological and contemporary timescales such as continued trophic downgrading due to loss of large-bodied mammals, but implications of those losses for local diversity patterns are less clear (39, 40).

Assessments of broad-scale temporal change in functional diversity have previously been limited by a lack of functional trait data. The majority of work has therefore focused largely on system-specific studies with traits collected *in situ*. This has challenged our ability to establish general rules for how functional composition may be changing through time, particularly in response to global change drivers. Ongoing efforts to assemble functional traits for a variety of taxa have made synthesis of existing community assemblage data and functional traits possible for the first time, providing initial insights into the ways functional diversity changes on a broad scale for specific taxa (e.g. fish, 41, birds, 42, 43). However, to date there has been no cross-taxa assessment of temporal functional change for a broad geographic and taxonomic extent (44).

Here we perform the first multi-taxa, multi-realm assessment of functional diversity change through time. We focus on mammal and bird species as a significant subset of the world’s biodiversity heavily impacted by anthropogenic change. While examining trends in plants, invertebrates, and other vertebrate species is of equal interest, trait data for those taxa raise additional challenges such as limited and biased species coverage (45), a lack of accepted species-level means, and differences in the types of traits collected. In order to ensure comparability across taxa in trait type and data quality we therefore focus on mammals and birds. Traits were intentionally selected to be representative of a species’ Eltonian niche, thereby summarizing the functional role they play in the community (46). An initial assessment of amphibian trends is included in the supplement, but excluded from general trend assessment here due to limited geographic coverage.

We assess thousands of mammal and bird functional diversity time series to determine whether or not there is a general trend of functional change, both in observed metrics and in metrics corrected for changes in species richness. We further assess the prevailing modes of change occurring at the study level to determine how functional change is related to species patterns, and which kinds of species and functional change are most common across communities. We distinguish between three possible scenarios of functional change: 1) significant functional change accompanied by changes in species-based metrics, 2) maintenance of functional

structure despite significant species changes, 3) maintenance of functional and species metrics. Based on expectation due to human impacts, we expect to find significant functional changes, often accompanied by species change.

2 Material and Methods

2.1 Data

We obtained mammal and bird time series from the BioTIME database, a global repository of high quality assemblage time series. All studies included in the database follow consistent sampling protocols and represent full assemblages rather than populations of single species (36). All time series include abundance of observed species. Following best practices for the database (47), studies with multiple sample locations were split into individual time series following a standardized spatial scale. Scale was set by a global grid with cell size determined based on the sample extent of studies with only a single location (see 36 for details on how sample extents were defined), with the area of each cell set to one standard deviation away from the mean of the single extent locations. All samples from a study within a single cell were considered to be a single time series, and species abundances were combined for all samples.

We used trait data from the Elton Trait Database, which consists of species-level means for traits that represent species' multifaceted role in the community (46). Traits include: body mass, diet, active diel period, nocturnality, forest foraging strata, pelagic use. Multiple traits (i.e. diet, foraging strata, activity seasonality, active diel period) were broken down into percentage or binary use for each level.

In order to ensure taxonomic consistency across datasets, BioTIME species were paired with trait data based on their species identifier from the Integrated Taxonomic Information System database (retrieved 09-15-2020 from the on-line database, <https://doi.org/10.5066/F7KH0KBK>), obtained through the `taxadb` R package (48, 49). If more than one species in the assemblage data resolved to the same identifier, observations were considered the same species. For trait data, traits for all species of the same identifier were averaged. Only studies for which at least 75% of species had trait data were included. In order to have a sufficient number of species to calculate functional diversity metrics, years with fewer than 5 species observed were also excluded. Sensitivity analyses were conducted for the trait coverage threshold and the duration of included time series.

Many studies had a variable number of samples within years. To account for this inconsistency in sampling effort we used sample-based rarefaction by bootstrap resampling within years for each time series based on the smallest number of samples in a year for that time series.

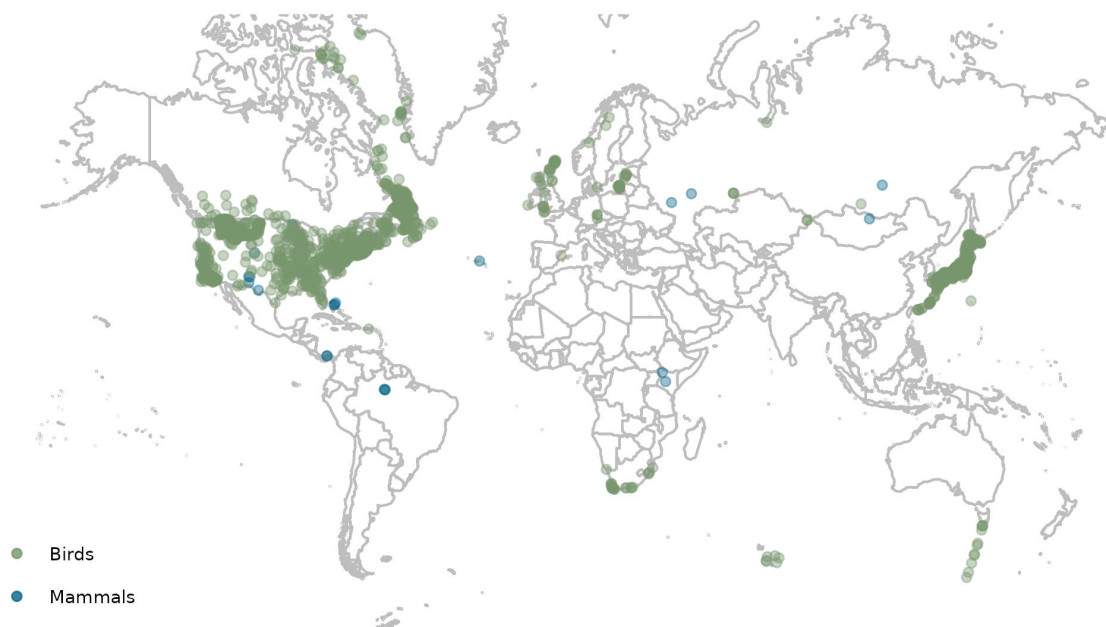
Our final dataset included 2,432 time series from 50 studies in 21 countries and 12 biomes and 6 different traits (Fig 1). Data came from both terrestrial and marine realms and five climates (Global, Polar/Temperate, Temperate, Temperate/Tropical, Tropical). The earliest sample was in 1923 and the most recent was in 2014. For a full breakdown of studies and their characteristics, see the supplement.

2.2 Diversity Metrics

We calculated yearly metrics of functional and species diversity for each time series. Species-based metrics include species richness (S) and Jaccard similarity (J) as a measure of turnover. Jaccard similarity was calculated relative to the first observed year for a time series. A negative trend in J would therefore indicate increasing turnover. We did not impose a correction for unobserved species as non-parametric estimators do not assign species identities to corrected richness values, and therefore could not be propagated to the functional diversity metrics.

Functional diversity metrics were calculated using the `dbFD` function from the `FD` R package (50). Here we report functional richness ($FRic$), functional evenness ($FEve$), and functional divergence ($FDiv$) which together describe three complementary characteristics of the functional space (22, 51). $FRic$ assesses the volume of the trait space occupied by species in the community, with higher values indicating communities with species of more extreme trait values. $FEve$ describes how species are distributed across the trait space and how abundance is distributed across species. Higher values of $FEve$ indicate more even spacing of species in the trait space and individuals across species. $FDiv$ measures the degree to which species and their abundances maximize differences in the functional space. Higher values of $FDiv$ therefore correspond to communities where many highly abundant species are on the edges of the trait space. We also calculated the community-weighted mean (CWM) of included traits to examine shifts in the distribution of each trait.

A



B

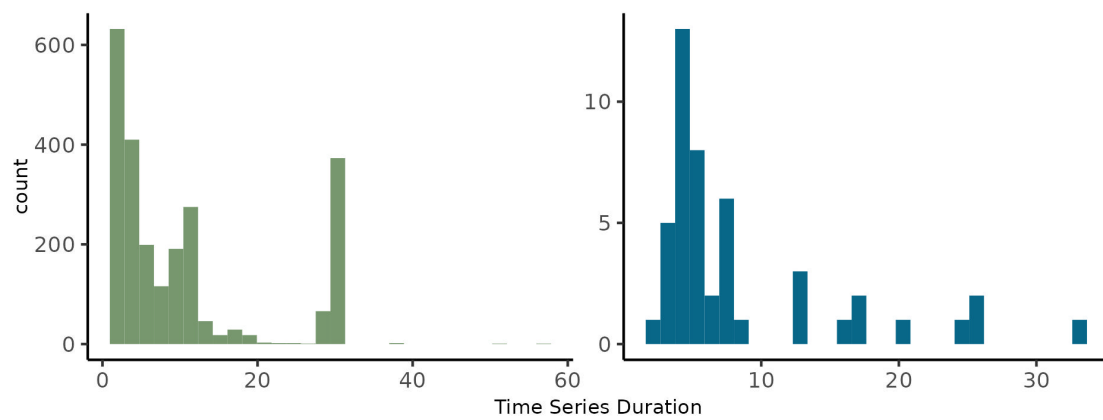


Figure 1: A) Map of time series locations with points colored by taxa, and B) histograms of time series duration broken down by taxa.

All available trait data for each study were included in functional diversity calculations with the exception of traits that were the same value for all observed species in the study. For variables with multiple levels each level was included as a separate trait axis. Continuous traits were z-score scaled to give each trait equal weight in the trait space (52, 53). The number of trait axes was limited to the maximum number of traits that fulfills the criteria $s \geq 2^t$, where s is the number of species and t is the number of traits. This restriction allows for a sufficient number of axes to capture the trait space while maintaining computational feasibility (54). Metrics incorporated weighting based on species abundance.

2.3 Null Models

To assess functional change independent of species richness we calculated the standardized effect size (SES) for each of the three summary functional diversity metrics (*FRic*, *FEve*, *FDiv*) from null estimates (55). Null model corrections allow us to assess the degree to which the observed functional diversity metric deviates from the value expected by chance in a randomly assembled community. Null estimates were calculated for each rarefied sample by randomly sampling species from the species pool for each year and randomly assigning observed abundances to species. Species pools included all species observed for a time series. This process was repeated 500 times to get an estimate and standard deviation of the null expectation for the metric for each rarefaction sample for that time series. We used these values to calculate SES using the following formula: $SES = [F_{obs} - mean(F_{null})]/SD(F_{null})$. We then calculated the median SES estimate for each metric from all the rarefaction samples for a time series. SES estimates can be interpreted as how much of the functional characteristic (richness, evenness, divergence) was observed beyond what was expected by chance for a community of that species richness.

2.4 Analysis

We estimated general trends for each diversity metric using a linear mixed effects model with a random slope and intercept for each study and each time series nested within the study. We fit 18 individual *CWM* models. All time series with data for a given trait were included in the corresponding *CWM* model. We estimated study level trends using individual linear models. For studies with more than one times series we fit a random slope and intercept for time series. Some study-level models could not be fit for five studies for at least one metric due to data limitations, but those studies were still included in the general models. They represented 12 of 1350 study-level models fit for each metric. For further details see the supplement. Where appropriate, response variables were \log or $\log(x + 1)$ transformed to better fit model assumptions of residual normality.

To test for trends within and between different levels of taxa, biome, and realm we fit separate models with each of those factors added as a predictor to the original model structure. We estimated within-level slopes and calculated between-level contrasts using the *emmeans* package (v1.8.2, 56). We assessed the impact of time series duration and start year on study-level trends using linear models with duration and start year as predictors. We also assessed the impact of potential study-level outliers on general trends. Details on that process can be found in the supplement. All models in our analysis were fit using the *lme4* (v1.1-30) package in R (v4.2.3) and p-values were calculated by Satterthwaite's degrees of freedom method using the *lmerTest* (v3.1-3) package with a significance level of $\alpha = 0.05$ (57–59).

3 Results

We found no significant overall trend in species richness or summary functional diversity metrics (observed or standardized) (Fig 2). We did find a significant overall decrease in Jaccard similarity, indicating accumulating changes in species composition. Non-significant overall trends indicate that although some studies experience increasing or decreasing trends, the average trend across studies was plausibly 0 (Table 1). Trends for different taxa, biomes, or realms were also non-significant for richness and summary functional diversity metrics, with the exception of a significantly increasing trend for functional evenness of global studies (characterized by having samples on multiple continents), and a significantly decreasing functional richness slope for temperate/tropical studies and mammal studies. However, trends were not exhibited for the standardized metric indicating that differences were largely due to changes in species richness. Further, with only two global studies, the trend should not be considered truly general. The general trends for *CWM* models were similarly not significant, with a significant positive trend for only percentage of fish in diet composition.

We did find significant differences between taxa, realms, and climate for Jaccard similarity and some of the *CWM*'s. For example while Jaccard similarity was decreasing in the general trend and there were significant within group slopes for Mammals, Birds, and Terrestrial communities, there was no significant slope for the

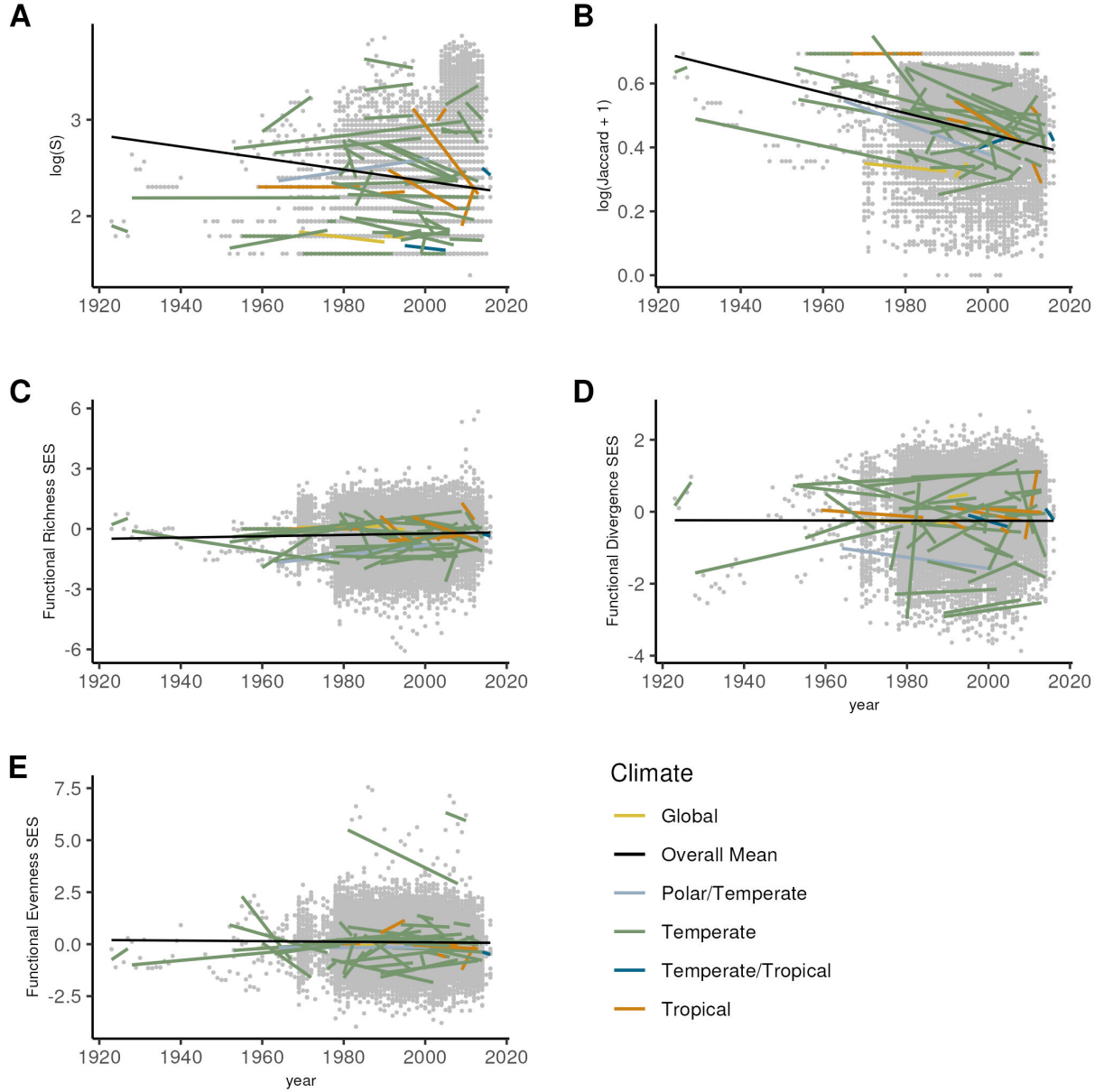


Figure 2: Plots of time series-level trends with line color corresponding to climatic region, with data points in grey and the overall metric mean in black for A) log species richness, B) Jaccard similarity, C) Functional Richness SES, D) Functional Divergence SES, and E) Functional Evenness SES

Table 1: Model estimates and statistics for general trend models for species richness, Jaccard similarity, and standardized functional diversity metrics. Additional model estimates, including CWM models, can be found in the supplement.

metric	effect	grouping	term	estimate	std.error	p.value
SES_FDiv	fixed		Intercept	-0.25	0.11	0.03
			Year	0.00	0.04	0.96
	random	study	SD Intercept	0.60		
			SD Year	0.11		
			Corr(Intercept, Year)	-0.16		
		time series within study	SD Intercept	0.60		
			SD Year	0.23		
			Corr(Intercept, Year)	-0.01		
SES_FEve	fixed		Intercept	0.09	0.16	0.59
			Year	0.00	0.01	0.73
	random	study	SD Intercept	1.04		
			SD Year	0.02		
			Corr(Intercept, Year)	1.00		
		time series within study	SD Intercept	0.40		
			SD Year	0.17		
			Corr(Intercept, Year)	-0.21		
SES_FRic	fixed		Intercept	-0.26	0.07	<0.001
			Year	0.04	0.04	0.35
	random	study	SD Intercept	0.29		
			SD Year	0.11		
			Corr(Intercept, Year)	-0.27		
		time series within study	SD Intercept	0.54		
			SD Year	0.18		
			Corr(Intercept, Year)	0.06		
log(Jaccard + 1)	fixed		Intercept	0.46	0.02	<0.001
			Year	-0.03	0.01	<0.001
	random	study	SD Intercept	0.09		
			SD Year	0.02		
			Corr(Intercept, Year)	-0.35		
		time series within study	SD Intercept	0.08		
			SD Year	0.02		
			Corr(Intercept, Year)	0.05		
log(Species Richness)	fixed		Intercept	2.40	0.10	<0.001
			Year	-0.06	0.05	0.17
	random	study	SD Intercept	0.64		
			SD Year	0.27		
			Corr(Intercept, Year)	-0.70		
		time series within study	SD Intercept	0.21		
			SD Year	0.09		
			Corr(Intercept, Year)	0.34		

marine realm, indicating that the general trend is mostly driven by turnover in terrestrial communities. For bird communities, we also found within group trends and between group differences for trends in foraging behavior. We found a significant increasing trend in utilization of the canopy in Tropical communities that was significantly different from the trends for Polar/Temperate and Temperate communities. There was a significant decrease in utilization of the understory for Terrestrial communities and significant increase in foraging below the water surface for global studies (but see the previous limitations of Global data). There was also a significant positive slope for *CWM* body mass for the single Temperate/Tropical study (with three time series) which were marine mammal communities.

We found significant dietary shifts across communities, with a significant increase in fruit consumption in Terrestrial communities and a significant decrease in nectar consumption in Tropical communities, a trend significantly different than that for Terrestrial communities. There was a significant increase in seed

Table 2: Number of studies that experienced a significant trend in each calculated metric out of 50 total studies.

	S	Jaccard Similarity	FRic	FEve	FDiv	SES FRic	SES FEve	SES FDiv
+	7	0	7	5	3	4	4	3
-	8	11	8	6	5	2	6	2

consumption in bird species, which was significantly different from the trend for Mammal communities. There was a significant increase in fish consumption for the two Global studies. Vertebrate consumption significantly decreased for Marine studies and for studies of Global and Tropical communities.

At the study level, 15 of 50 studies exhibited a significant trend in species richness and 11 exhibited significant turnover. For observed functional metrics, 25 of 50 studies exhibited a trend in a least one metric, and 15 of 50 studies exhibited a significant trend for at least one standardized metrics (Table 2). In general, there were more significant trends for uncorrected metrics, with some disappearing after correction, indicating that those trends were likely due to changes in the number of species. Hypothesis testing for study-level trends is likely affected by multiple testing issues and some trends identified as significant are therefore potentially spurious. Rather than interpreting changes in specific studies, we present these results as a general picture of the kinds of trends experienced by communities.

Study-level slopes for summary functional metrics were significantly related to start year of the time series for Jaccard similarity and functional evenness, both of which had significantly more negative slopes with more recent start year. No summary functional metrics were significantly related to the start year of the time series.

We assessed the sensitivity of general trend results to major data processing decision by rerunning models with increasingly conservative subsets of the data. After excluding time series with less than two, three, and four year durations, we found that the general trend for increase in CWM aerial foraging disappeared, but two other trends in CWM's appeared. After excluding time series two years long, a general trend appeared for increased CWM use of the forest canopy, and decreased CWM of seed consumption. These two trends remained as increasingly shorter time series were excluded suggesting the increase in aerial foraging was an erroneous finding while the other two trends were more robust. Percentage of species in a community with trait data did not appear to have an affect on general trend results, as general trends were unchanged with increasing cut offs for percentage of species with trait data. A complete list of models run in the sensitivity analysis and their results can be found in the supplement.

4 Discussion

Our study represents the largest broad-scale multi-taxa assessment of functional change through time to date, giving a first look at aggregate and local trends in functional diversity in mammal and bird communities. Surprisingly, we did not detect an overall trend in any of the summary functional diversity metrics. As with previous species-based syntheses, we also found no overall trend in species richness accompanied by increasing turnover through time (36), indicating that non-significant trends in functional metrics may be consistent with similar well-documented species derived trends. We found no trend in functional change for almost all realms, biomes, and taxonomic groups, with evidence of functional richness loss in mammal studies only. These results are consistent with multiple studies linking anthropogenic drivers to loss of functional diversity in mammal communities (60–62)

Despite a lack of general trends in summary functional metrics, we did find multiple trends in *CWM*'s for studies coming from the same taxa, realms, or climates, many of which are consistent with previous findings for those contexts. For example, the decrease in insect consumption for tropical communities reflects well documented declines in tropical insectivorous birds (63). Reduction in utilization of understory foraging for terrestrial communities could be the result of disturbance like human recreation or increased predation from introduced species. Other shifts in diet for both Birds and Mammals, including increasing fruit, seed, and vertebrate consumption and decreasing seed consumption in some climates point to important areas for further exploration.

At the study level, biodiversity change fell into four dominant scenarios of change based on trends in richness, turnover, and functional metrics: no change, only functional change, richness and functional change with

turnover, and richness and functional change without turnover (Table ??). Around a quarter of studies experienced no trend in richness, turnover, or functional metrics. These studies spanned the distribution of study durations excluding only the very longest running studies, with the longest no change time series lasting 23 years.

Another quarter of the studies showed no trend in richness or turnover, but did show a significant shift in at least one summary functional metric. These communities are best aligned with scenarios of species replacement where only a few functional outliers replaced functionally indistinct species or vice versa (there were studies with positive and negative trends in all three functional metrics). Studies in the scenario of only functional change were heavily skewed toward shorter running time series, indicating that they may represent a limited snapshot of communities that on longer time scales would be exhibiting significant change in species based metrics, particularly as species replacement continued adding to turnover. Communities in this scenario, and the previous scenario of no functional change are consistent with hypotheses that species richness may be strongly regulated through time (3, 8), and emphasize that maintenance of functional structure can be divorced from those processes.

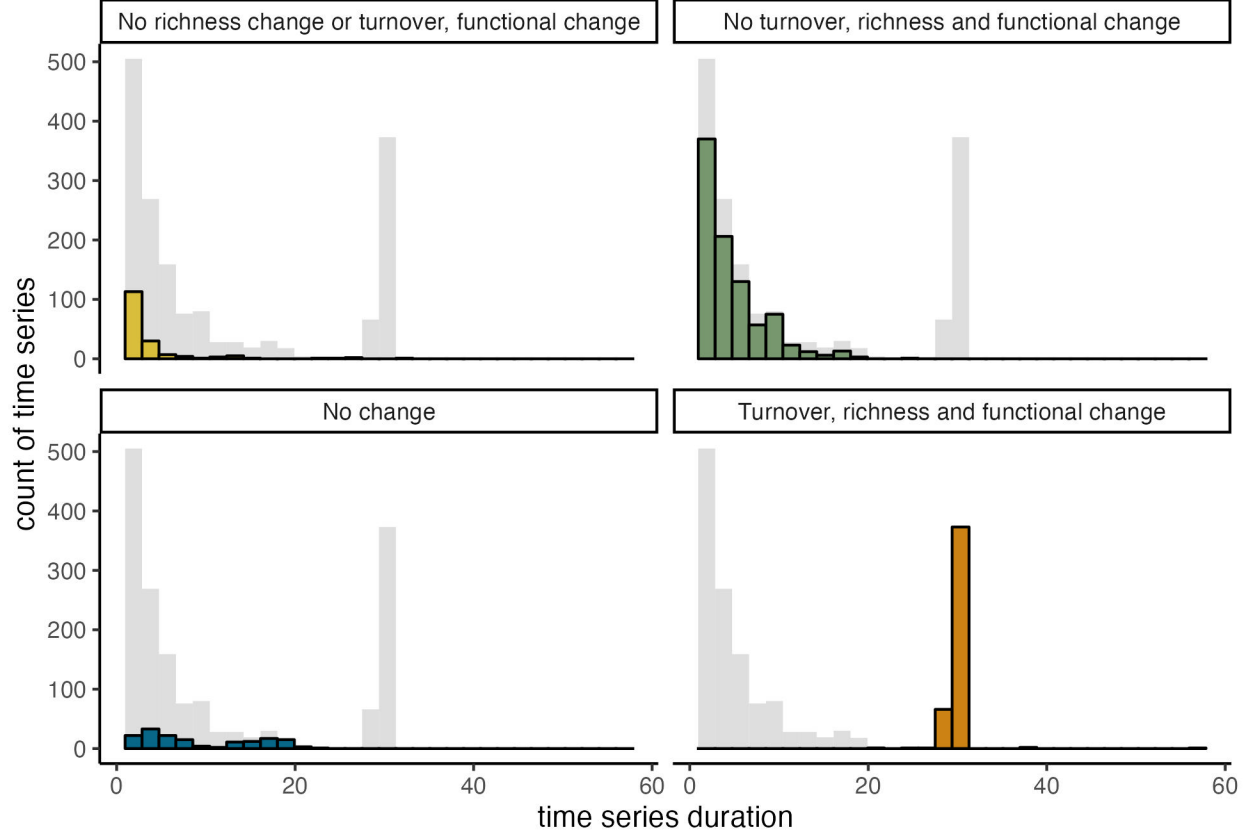
About 10 percent of studies, but the majority of time series in our dataset, exhibited richness and functional change but no turnover. These studies also spanned the the distribution of time series durations, excluding the longest running studies. With the exception of one study, trends in functional change for this group were only found for uncorrected metrics and disappeared after correcting for species richness, indicating that functional change in this group is almost exclusively the result of species gains or losses rather than turnover of species with different functional traits.

About 15 percent of studies, which were also exclusively the longest running studies, had a trend in turnover, richness, and functional change. The studies in this scenario fell into two groups: a positive trend in richness with a positive trend in functional richness (corrected and uncorrected), and a negative trend in species richness with a negative trend in uncorrected functional richness and no trend in corrected richness but a trend in other corrected functional metrics. This would indicate that when species are lost from a community, they are not more functionally unique than expected by chance, though they may produce shifts in other aspects of functional structure. When species are gained however, they disproportionately add to the functional richness of the community.

Our results illustrate the range of relationships between species-based and functional metrics observed in real communities. Critically, particularly for the short observation time windows that characterize the majority of ecological data, functional shifts may be underlying seemingly static species-based community metrics. Species-based approaches may therefore be missing areas where significant change in the functional space could be impacting ecosystem function and resilience. In scenarios where there are significant species gains or losses over time, we found evidence that species losses may be relatively functionally indistinct, while species gains contribute disproportionately to the richness of a functional space. This finding is consistent with evidence that at least in bird communities, common functionally general species are being lost even as rare species are increasing (64–66).

Our results are consistent with ecological expectations that community dissimilarity would be greater the larger the observation time window purely due to background processes, which is likely further accelerated by global change drivers (14). While we do not address how observed rates differ from background expectation here, we can make some assertions about the implication of turnover for functional change. Where turnover is occurring, it is almost always accompanied by a directional change in the functional space. Species are not therefore being replaced by exact functional counter parts. The fact that we observed both increases and decreases in corrected functional richness accompanying turnover is a reminder that replacements are not always an indication of functional loss, but can also lead to increased functional richness. While shifts in functional space may be the result of environmental pressure, we cannot distinguish between directional change and shifts due to the unavailability of an analog species in the species pool.

Still, some results stand in contrast to predictions for trait shifts under global change. For example, mean body size is predicted to decrease as a result of climate change impacts and megafaunal loss (67), a phenomena which has already been well documented empirically and experimentally in multiple taxa (68–71). While the species-level trait means used here are not appropriate for assessing intraspecific body size shifts, we would expect to see shifts in community-wide means due to local losses of large-bodied species. Instead, we found no evidence of a trend in *CWM* body size, with the exception of a single study of marine mammals in the Bahamas which showed a significant increase. Still, many of the studies in our dataset draw from areas that may have experienced significant loss of large-bodied species before the observation window, with contemporary loss rates slowing (72). Trends could be significantly different for the same time periods in



		No Richness Change	Richness Change
Functional Change	No Turnover	12	6
	Turnover	2	7
No Functional Change	No Turnover	11	1
	Turnover	1	1

Figure 3: Comparison of the distribution of time series durations from each type of change to the overall distribution of time series durations, with no richness change or turnover and functional change in yellow, no turnover but richness and functional change in green, no change in blue, and turnover, richness and functional change studies in orange.

regions of sub-Saharan Africa, for example, which has poor representation in our dataset but where megafauna exist on the landscape and are increasingly threatened (73).

What does local maintenance of functional structure mean for ecosystem function? The vast majority of experimental and observational work links declines in function to declines in functional or species diversity (7, 18, 74). By those criteria very few communities in our dataset are in a state of concern for loss of functionality (Table 2), though we did find evidence that mammal communities may be in greater danger than bird communities. Still, shifts in metrics are only relevant if the underlying traits are those most critical for ecosystem function. We were limited in this analysis to the traits available rather than those with strong empirical links to function. Similarly, the dimensions of functional space most important for ecosystem function are still a topic of on going debate, and at least some known aspects important for multifunctionality were not measured here (e.g. dispersion, rarity, abundance of dominant species, 75).

4.1 Potential Methodological Limitations

Here we approach the question of functional change using the best available data and biodiversity synthesis approaches. While we found signatures of change at the study level, some gaps in best practices may be obscuring a true general trend at the aggregate level. First, the BioTIME database, while the most comprehensive data source of time series available, is limited in temporal and geographic scope. Most time series span only a few years (Fig 1) and may not provide the statistical power necessary to detect trends (76). The database is also not a representative sample of the world’s biodiversity or areas of greatest threat (6, 12), and the subset of data in this study is predominantly from North America. We may simply not have data from those areas experiencing the greatest perturbation (77), particularly scenarios of conversion to urban, human-dominated landscapes. While evidence from other work shows even disturbed communities can maintain functional structure (32, 34), these results should not be interpreted as evidence of low functional impact in areas of heavy human disturbance.

Second, despite using the most comprehensive trait databases for these taxa, we were still limited to species-level means of the traits deemed important by database creators. The importance of intraspecific variation is well documented (78, 79), however individual-level traits are rarely collected alongside monitoring data, especially for the longest running efforts. Species-level traits may be obscuring more subtle shifts in the trait space happening within species. Likewise, available trait data may not capture the traits experiencing the greatest change. For example, we focus here mostly on ecological traits (i.e. foraging strategy, diet, etc) rather than life-history or reproductive traits.

Third, while we use here the most common metrics for describing functional diversity, they do not measure some potentially important aspects of the functional space. Most notably, the summary metrics we calculated do not capture shifts in the location of the functional space as a whole. For example, two communities could have very similar metric values but no overlap in their trait spaces. This is especially relevant in the context of biodiversity change as a species loss could be replaced by a species with very different functional attributes, but the replacement would go undetected if the new species expanded the trait space by the same degree and had similar abundance. This scenario may be common in communities tracking changing environmental conditions. While trait CWM’s capture axis shifts, approaches for assessing multidimensional shifts in functional space are still relatively new (54, 80, 81) but could shed critical insight into functional composition changes of this nature.

4.2 Policy Implications

While we found no over all trends in functional metrics, our results should not be interpreted as an indication that the ongoing biodiversity crisis is less severe than previously described, or that there is no concern for functional change as a result of anthropogenic impact. In fact, study-level trends indicate quite the opposite, that functional shifts with unknown implications for ecosystem processes may be going undetected by common species-based approaches, particularly for short observation time windows. While the majority of studies in our dataset did not experience a significant functional loss, a substantial body of work links functional degradation to species losses as a result of direct human intervention in the form of land use change and intensification or habitat fragmentation, indicating that those studies are simply not representative of the kinds of impacts of greatest policy concern (31, 82, 83).

4.3 Future Work

We present here four prevailing scenarios of change experienced in bird and mammal communities. While we offer an first discussion of which kinds of change are most common and why, assessing the true global prevalence will require continued efforts to fill data gaps, a well recognized challenge in ecology (6, 12, 77). Still, a “scenarios of change” framework can provide structure for future work addressing functional shifts, particularly as we reconcile results from broad-scale syntheses with in-depth single system studies. It will be particularly critical to link forms of change to individual drivers to assess which drivers may impact species and functional diversity differently. Understanding those links will help identify where directly measuring functional structure instead of just species change is necessary for understand impacts on a given system. In addition, direct links to drivers will improve our ability to distinguish between communities experiencing no change due to a lack of perturbation from communities with high resilience in the face of disturbance.

Here we identify trends that are statistically significant, however they may not necessarily be ecologically significant. While it is common to link changes in functional metrics to changes in ecosystem processes, those changes are less frequently discussed in terms of the size necessary for ecological impact. The degree of change in a process considered ecological meaningful is somewhat subjective and a function of the system and management context, making identifying the ecological meaning of broad-scale aggregate shifts even more challenging. It is further hampered by the use of species-level trait data, as the traits most closely linked to a process of interest may not be available (84). Future trait collection that explicitly considers existing frameworks for linking traits to processes (e.g. the response and effect framework 15) would facilitate improved ecological interpretation of potential functional changes.

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